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Author's address: W. BERGMANS, Instituut voor Taxonomische Zoölogie (Zoölogisch Museum), Plantage Middenlaan 53, Amsterdam-1004, The Netherlands

New systematics and the classification of Old World *Hipparion*

By ANN FORSTÉN

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The ideas of the New Systematics (HUXLEY 1940) are presently generally applied in the classification of recent birds and mammals. The recognition, at the beginning of the century, of the polytypic species greatly simplified classification and facilitated inferences as to the interrelationships of the species. Geneticists early emphasized the fact that species are composed of populations (DOBZHANSKY 1937), of which no two are identical in their genetic and morphological make-up, due to initial differences in the frequency of genes and local differentiation, but between which similarities tend to be preserved because of initial qualitative genetic similarities and genotypic buffering, migration and marginal interbreeding. In some branches of classification, especially the classification of birds, the typologically defined, monotypic species had already then been demolished, and emphasize had been laid on the subspecies and the local populations of species. MAYR (1942) discusses at length the concept of the polytypic species as reflecting a population thinking in systematics.

The modern systematist uses samples drawn from populations for description and comparison of populations in and between species. Often quantitative methods are used to measure the range of variation in, and for statistical comparison of, samples. The type, earlier the main or only basis for characterization of the species, is considered just a name-bearer, but otherwise no more characteristic of the species than any other specimen from the sample, since in animals which reproduce sexually no two individuals, except identical twins, are exactly alike, and no individual can be more typical of the species than any other. In addition to morphological characters, features of physiology, ethology, geographical occurrence etc. are important in comparisons. In short, the pigeon-holing of species of the Old Systematics has given way to a biological evaluation of the species of the New Systematics. This tema has, since MAYR's important work of 1942, repeatedly been discussed (MAYR 1943, 1949, 1958, 1963; MAYR, LINSLEY and USINGER 1953; SIMPSON 1943, 1951, 1961), as has the application of the New Systematics in paleontology (ARKELL and MOY-THOMAS 1940; JEPSEN, MAYR and SIMPSON [edits.] 1949; NEWELL 1948; SIMPSON 1943; SYLVESTER-BRADLEY 1951; SYLVESTER-BRADLEY [edit.] 1956). The systematists taking part in the discussion have almost unanimously agreed to discard the static, typological species-concept in favor of a concept of a dynamically evolving species, which consists of local populations, each with their own gene pool, intergrading with neighbouring populations.

According to the New Systematics, thus, the species „consists of a group of populations which replace each other geographically or ecologically and of which the neighbouring ones intergrade or interbreed whenever they are in contact or which are potentially capable of doing so“ (MAYR 1964, p. 120). In SIMPSON's (1951) words “A phyletic lineage evolving independently of others, with its own separate and unitary role and tendencies is a basic unit in evolution”.

The polytypic species concept has not been generally adopted in paleontology, and pigeon-holing classification, based mainly on morphological criteria, still prevail. The usual excuses for this practice are that it is impossible to know whether finds are exactly contemporaneous and that a wide species definition makes specific identification of new finds difficult, since it allows for a range of morphological variation. The species in paleontology, accordingly, seldom has dimensions in time or space, it mainly has a point-like distribution and is known from a vertically limited level only. Thus paleontological systematics have remained typological, since other criteria than morphological ones, such as the possibility of ecological or geographical replacement, as mentioned in MAYR's definition of a species, or the criterion of “separate and unitary evolutionary role and tendencies“ as in SIMPSON's definition, are not taken into account when species are described. It is maintained that species in paleozoology cannot be defined according to the same criteria as in neozoology, yet horizontal and vertical speciation (i. e. speciation in space and time) are probably inseparable in nature; they cannot be separated in fossil forms, but it is debatable whether they can in recent forms either, since time is necessary for differentiation (NEWELL 1948).

This is the situation in the systematics of the Old World fossil equid genus *Hipparion*. Ever since 1829 when the first finds were described by v. MEYER, new materials have been reported on and new species described at an increasing rate. Up to about 1930 new species had been described at a mean rate of one every three years. At that time a certain reaction set in, and doubts were voiced against the practice of describing each new find as a new species. TERIAEV (1936), for instance, went to the opposite extreme and maintained that all species of *Hipparion* described so far in fact were only local forms of a single, wide-spread species. This reaction against the excessive splitting of the genus should be seen against the background of the dawning New Systematics. However, the ideas of the New Systematics did not take root among Old World paleontologists; although almost every worker in the group since 1930 has pointed out that the number of species described in the genus *Hipparion* is too large, the mean rate of increase in the number of new species has since been two every three years. There have seldom been attempts to syntheses or to conclusions as to the interrelationships and evolution of these “species”. The main interest has been the description and pigeon-holing of materials. Although some quantitative methods often are used for evaluation of the variation in a sample, in comparisons of forms local morphological differences are given more weight than overlap and similarities, and not enough heed is taken of allometric growth-relations. One has the impression that what is studied and compared is not so much variable samples (hypodigms in SIMPSON's [1940] terminology), as individual specimens (i. e. types of the Old Systematics).

A study of the material of *Hipparion* from some two hundred localities in Europe, Africa, and Asia, definitely shows that some local forms are more closely similar to each other than they are to other such forms. Useful morphological features according to which grouping of forms can be done are, among others, overall size, robustness and proportions of the limbs, development of the cuneiform facet on MT III, degree of hypsodonty, complication of the enamel, and development of cingular structures in the cheek teeth. The similarities between forms of one group are not only morphological, but are apparent also in characters such as geographic and geo-

logic occurrence, and probable habitat preference. Although there is wide overlap in occurrence, in habitat preference there is little overlap between groups. All morphological characters vary independently between local forms of one group as well as between groups; the differences between groups, thus, are gradual rather than absolute. However, there is an average condition which characterizes each group, and where forms of different groups occur in the same local sample they are usually distinct and separable. This is, for instance, the case with the two forms of *Hipparion* occurring in the fossil sample from Pikermi, Greece. Although it has frequently been maintained that the metapodials from Pikermi form a single scatter of observations if total length is plotted to distal or proximal breadth, and moreover, that correlation between these measures is negative (i. e. that the shortest bones are the broadest, the longest the narrowest), this is not supported by the data. In a large sample of metapodials from Pikermi two scatters are evident for each variate, and although there is some overlap in proximal breadth between the scatters, there is none in distal breadth. In each individual scatter correlation is positive. Thus, the two forms represented in the sample differ in proportions of their metapodials, and, in fact, of all other long bones studied.

Inferences as to the ecological habitat preference of different forms of *Hipparion* are based on the observed correlation of certain morphological features of these horses and the inferred ecology of the associated fauna. Certain fossil faunal elements, such as deer, pigs, and mastodonts, are usually believed to indicate a sylvan faunal assemblage, and elements such as hypsodont antelopes and gazells, and ostriches to indicate a savanna-steppe assemblage. In some cases these assumptions have been confirmed by finds of fossil plants in the same beds as the animals. On the other hand, there have been doubts expressed as to the reliability of such conclusions about the ecology of fossil animal assemblages, as the fossil fauna does not necessarily correspond to the once living one, due to transportation and mixing (SONDAAR 1968). The frequent occurrence of robust, heavily built *Hipparion* with richly plicated enamel and well developed cingular structures in faunas of a sylvan character has long led paleontologists to believe in a real association of these morphological characters with "forest-adaptation" in *Hipparion*. Similar features do, however, also occur in *Hipparion* in typical steppe assemblages. In the steppe faunas, but not in the forest faunas, also occur dwarf forms and forms showing combinations of morphological features which are almost antithetical to those of forest-hipparion, i. e. slim built, simple enamel pattern, and comparatively little developed cingular structures. All these presumably ecologically correlated characters show average differences not only between groups of forms, but also to some degree between local forms of one group, especially in what appears to be a temporal sequence of forms. Thus all forms of *Hipparion* described from geologically early faunas are robust and heavily built, and also have other forest-*Hipparion* characters in common; in fact they are the forest-*Hipparion*. In almost all cases the associated fauna indicates forest, and although the early finds are scattered, one cannot but conclude that this is a typical example of geographic and ecological replacement, and that early forest-*Hipparion* consisted of a single, wide-spread, polytypic species. As far as known this early form always occurred alone in the faunas where it has been found. In faunas which are slightly younger and may represent ecologically different facies, judging from the appearance of the horses and from the other faunal elements, two or three forms may occur sympatrically, but between them there are usually characteristic differences in size, proportions, and visual morphology, as already discussed in *Hipparion* from Pikermi and in the steppe and forest-hipparions. In almost all of these faunas there are forms which resemble early forest-*Hipparion*, and share characters in common with the latter, in addition to showing some modernizations, for instance in the

foot and the teeth, which resemble steppe-*Hipparion*. The presumption that these forms represent the direct descendants of early forest-*Hipparion*, with similar adaptations slightly "modernized", lies close at hand. Steppe-*Hipparion*, of which there are several different local forms, seems to have evolved from early forest-*Hipparion* through intermediate forms, and gradually to have evolved the adaptive features of the steppe forms. As is the case with the early and "modernized" temporal forms of forest-*Hipparion*, these steppe-hipparions seem to form a chrono-cline culminating in some extremely long and slim-legged forms. The early steppe-hipparions may also have been ancestral to the dwarf-hipparions. The forms of the different groups, thus, may be arranged in lineages.

The pattern sketched in the foregoing discussion is roughly the same throughout the known area of distribution of Early Pliocene *Hipparion* in Europe, N. Africa, and the Mid East; much the same pattern can be traced as far east as India and Central Siberia. Pliocene forms known from the Far East, from China and Mongolia, may differ slightly in their closer affinities. In Europe forest-*Hipparion* seems to have continued on in conservative form, probably as late as Middle Pliocene; the dwarf forms and steppe-hipparion were confined to the Lower Pliocene. The evolution of the genus in the Late Pliocene and Early Pleistocene is not well known, due to the geographically scattered and rare finds, but there are indications of polytypic species with wide distribution, for instance in Africa (BONÉ and SINGER 1965). It can of course be maintained that the group similarities, here assumed to have been adaptations significant at the species level, evolved again and again in forms not closely related but occupying similar ecological niches in different faunas. Inherent in this belief is the belief in a lack of interchange between populations and in the strong localization of populations. There probably was some convergent evolution in *Hipparion*, for instance dwarf forms did evolve independently of each other in different parts of the area of distribution of the genus, and steppe-*Hipparion* characters probably evolved independently, for instance in the Mid and Far East. It has been stated that the same species of *Hipparion* cannot have occurred in Europe and Asia because of the marked differences of the faunas of the two continents (SONDAAR 1971), and that the morphological similarities thus are due to convergence, but differences in the associated faunas are not necessarily prerequisites for convergence and specific difference of allopatric forms, since subspecies of single species do occur in different faunas. The taxonomical differences between the Early Pliocene European and Asiatic faunas may be apparent, and due to ignorance of local paleontologists of the corresponding taxa in faunas in other parts of Eurasia resulting in splitting, rather than due to parallel evolution. There are no indications that *Hipparion* evolved independently in Europe and Asia. Descriptions of Asiatic materials (SEFVE 1927; GROMOVA 1952; OZANSOY 1965; FORSTEN 1968; HUSSAIN 1971; SONDAAR 1971) do not exclude a relationship, and in some instances they definitely indicate one. It is to be expected that increased geographic distance may result in increased differentiation of the marginal populations, but apparently Early Pliocene *Hipparion* from Turkey, Persia, the countries around the Caspian and Black Seas, Europe, and North Africa formed more or less continuous populations intergrading locally, and, at least at one time, also intergrading with populations as far east as India. Since differentiation did take place, i. e. the rise of steppe-*Hipparion* and the dwarf-forms, there must have been some geographical isolation of populations.

Differentiation in Old World *Hipparion* was adaptive. Long-time evolutionary trends appear to have been absent; for instance, there was no continued trend for increase in crown height, nor were there any continued size-trends. In the Early Pliocene there probably was a short-time trend for decrease in size in some lineages,

culminating in the dwarf-hipparions, and the Early Pleistocene forms were among the largest known, and although early forest-*Hipparion* was comparatively low crowned and the Pleistocene forms were markedly hypsodont, crown height increased at different rates in different lineages and reached maximum values already in some of the dwarf forms. As most morphological features, overall-size and hypsodonty fluctuated checker-board fashion throughout the history of the genus. The rise of the dwarf forms, as well as of the steppe and "modernized" forest-hipparions, is seen as the consequence of the opening up of a new or ineffectively occupied ecological niche, that of the steppe environment. Differentiation, thus, was spread into unoccupied sub-niches of the adaptive zone of the grazing horses, or episodic and of unknown significance, as the development of the peculiar nasal notch in "*Proboscidihipparion*". The segregation of the ectostylid in "*Stylohipparion*" is also regarded as episodic, although probably adaptive, but hardly more than of specific significance since the ectostylid was no new feature in the lowers of *Hipparion*, having been frequent in the early forest forms. Differentiation in the genus was speciation, and it is uncertain whether it reached the sub-generic level.

How is this pattern to be reflected in the classification of *Hipparion*? The usual, but not very fruitful, practice is simply to give every local find its own specific denomination, but this completely muddles the picture. The reasonable solution, it seems, would be to recognize the group similarities between finds, and to classify accordingly. If every local find is to have its own specific name, the groups would have to be classified at least as sub-genera; such a practice, however, would necessitate similar alterations in other genera of orthodox equid taxonomy, and would make taxonomy unnecessarily complicated without contributing anything to our understanding of the interrelationships of the species. A sounder solution would be to classify the groups as polytypic species with local populations differing in both space and time. By such a practice the species would conform to SIMPSON'S criteria for a "basic unit in evolution", i. e. "with its own separate and unitary evolutionary role". Also the area of distribution of each species would most probably be more realistic than the point-like distribution of the old, monotypic species. The simplified taxonomy proposed would enhance the dynamic aspect of the species and would better reflect the mode of evolution of *Hipparion* in the Old World.

Summary

There is need for a reevaluation of the systematics of Old World *Hipparion*. The constant description of new species, most of which are certainly synonyms, has proved utterly sterile; it has made taxonomy of the genus top-heavy, without offering any clues as to the interrelationships of these forms. Some possible solutions are here roughly sketched; the group similarities between local finds are emphasized and synonymization is recommended. The recognition of polytypic species in *Hipparion* would do away with the static, local species lacking dimensions in space and time, and would greatly facilitate inferences as to the evolution in the genus.

Zusammenfassung

Neue Systematik und die Klassifikation der altweltlichen Hipparionen

Die Systematik der Gattung *Hipparion* der Alten Welt muß kritisch überprüft werden. Die stete Beschreibung neuer Arten, von denen die meisten sicherlich Synonyme sind, hat sich als sehr unfruchtbar erwiesen. Sie hat die Taxonomie unübersehbar gemacht, ohne irgendwelche Einblicke in die Verwandtschaft dieser Formen gewährt zu haben. Einige mögliche Lösungen werden hier skizziert, die Gruppenähnlichkeiten lokaler Formen betont, und Synonymierung wird empfohlen. Falls in der Gattung *Hipparion* der polytypische Artbegriff die statische, lokale Art ohne zeitliche und räumliche Ausdehnung ersetzt, würden die Schlußfolgerungen die Evolution der Gattung betreffend in hohem Maße erleichtert.

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Author's address: Dr. ANN FORSTEN, Zoological Institute at the University of Helsinki, P. Rautatiekatu 13, 00100 Helsinki 10, Finland